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Failure of the Div. 2J3KL cod recruitment prediction using salinity

by

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ABSTRACT

Two published multilinear regression models for predicting year class strength in Div. 2J3KL cod are re-examined. It is shown that the salinity term in these models is no longer significant when the most recent (1993) analytical assessment results are used. As an alternative to regression models, nonparametric models incorporating spawner biomass as well as spawner biomass and salinity together are examined. The cross-validated prediction sums of squares is used to compare the predictive ability of alternative regression and nonparametric models with respect to both the 1992 and 1993 assessment estimates. The reduction in prediction sums of squares achieved by including salinity is highly significant for the regression model but only just significant for the nonparametric model when applied to the 1992 estimates. The reduction is not significant for either model when applied to the 1993 estimates. Although predictions of recruitment based on salinity are not currently useful, it is shown that spawner stock biomass is a reliable predictor and should be used when making stock projections.

RÉSUMÉ

On réexamine deux modèles publiés de régression multilinéaire servant à prédire l'abondance des classes d'âges de morue dans les divisions 2J3KL et on démontre que l'élément salinité de ces modèles n'est plus significatif quand on utilise les résultats de l'évaluation analytique la plus récente (1993). On examine également, comme solution de rechange aux modèles de régression, des modèles non paramétriques qui incorporent, d'une part, la biomasse de reproducteurs à elle seule et, d'autre part, la biomasse de reproducteurs et la salinité. La somme des carrés des prévisions, une fois contrevalidée, est utilisée pour comparer les valeurs de prévision respectives des modèles de régression et des modèles non paramétriques appliqués aux estimations établies d'après les évaluations de 1992 et 1993. La diminution de la somme des carrés que l'on obtient en incluant la salinité est très significative dans le modèle de régression, mais l'est tout juste dans le modèle non paramétrique en ce qui concerne les estimations de 1993. Quoique les prévisions de recrutement fondées sur la salinité ne soient pas utiles actuellement, on démontre que la biomasse de reproducteurs est une variable prédictive fiable, qui devrait être utilisée dans les projections sur les stocks.

Introduction

Year class strength depends on the initial number of eggs spawned and subsequent survival through to recruitment. The number of eggs spawned is linearly related to the weight of mature females (e.g. May 1967). Initial survival is partly influenced by females through the quality of the eggs and the way in which they are distributed in time and space, and by males through fertilization rates. Following spawning and fertilization, survival is determined largely by the "environment", i.e. factors other than those related to the parent population, although cannibalism and intraspecific competition (density-dependent factors) may also have an effect. The large fecundity of many fish species is indicative of the uncertainty in survival to maturity.

It has been a traditional pursuit of fisheries scientists to try and explain a significant proportion of the variability in recruitment using one or more environmental variables. Generally these variables are computed as annual averages from multiple samples at one or more locations in the habitat throughout all or part of the year. When significant relationships have been found between year-class strength and the environment, these relationships have seldom been examined in terms of their ability to predict values not included in the fit. Cross validation is one possible approach to looking at a model's predictive ability. A single value is left out of the fit. This value is then predicted based on the fit to the remaining values. The procedure is repeated for each value in turn and the prediction sums of squares (PSS) computed. Cross validation may show that, while the environmental variable improves the fit, it does not significantly improve the PSS relative to the PSS based on estimated spawner stock size alone or based on the geometric mean of estimated past recruitments.

Rice and Evans (1986) provided evidence using a nonparameteric approach that recruitment (number of fish surviving to age 3, the age at first capture in the fishery) in the Div. 2J3KL cod stock is influenced by spawning stock biomass. Principal components analysis of the residuals from the nonparametric model showed a relationship with water conditions (temperature and salinity as measured at station 27) in spring and early summer. Predicted recruitments based on spawner stock alone were too low when March and June surface waters were relatively cold and saline. In an earlier study, Sutcliffe et al. (1983) also examine the potential effect of salinity on recruitment, but without first accounting for the spawner stock effect. They found that a multilinear regression model including depth averaged (0-50m) summer time (July-September) salinity measurements from station 27 for the three years following spawning explained 80% of the estimated recruitment variability from Wells and Bishop (1980) for the period 1958-76. Myers et al. (1993) found that predictions from the fitted Sutcliffe et al. (1983) model appeared to be well correlated with subsequent recruitment estimates, explaining 49% of the variability in recruitment as estimated in the Baird et al. (1992) stock assessment. Further, Myers et al. (1993) found that the regression that provides the most reliable prediction of recruitment for the Div. 2J3KL stock includes both spawner biomass and salinity as explanatory variables. They suggest this model provides an alternative to the convention of using the geometric mean of past values of recruitment for short-term projections in stock assessments.

In this paper we examine the predictive ability of the Sutcliffe et al. (1983) model using the 1993 assessment in Bishop et al. (1993). We also also refit the Sutcliffe model to the Baird et al. (1992) and Bishop et al. (1993) estimates of recruitment. We examine the Myers et al. (1993) model in detail with respect to both the 1992 and 1993 assessment estimates, paying attention to the cross

validated PSS. We also utilize a randomization test to determine the significance of the salinity term. An alternative nonparametric model following the approach of Rice and Evans (1986) is examined in similar detail. Conclusions are then drawn regarding the utility of predictive models of Div. 2J3KL recruitment based on spawner stock and salinity.

Sutcliffe's model

The Sutcliffe et al. (1983) model is

$$\text{Recruitment}_y = -26360 + 162s_y + 278s_{y+1} + 406s_{y+2}$$

where Recruitment is numbers of 4 year olds x 10^6 and s_y is 0-50m depth-averaged summer (July-September) salinity at Station 27 in year y. In Fig. 1 the Sutcliffe model with parameters as estimated by Sutcliffe et al. (1983) is used to predict recruitment up to 1992. Also plotted are the 1992 (Baird et al. 1992) and 1993 (Bishop et al. 1993) estimates of numbers of 4 year olds. Superficial examination suggests good correspondence, although there is an increasing divergence between predicted and estimated number of 4 year olds after 1970. Scatter plots of estimated versus predicted values for the two assessments (Fig. 2) illustrate the variability more clearly. The range in estimated recruitment is more than a factor of three at intermediate levels of predicted recruitment. Myers et al. (1993) report that Sutcliffe's model accounts for 49% of the estimated number of 4 year olds in the 1992 assessment. The amount of variance explained declines to only 25% for the 1993 assessment estimates.

Sutcliffe et al. (1983) fitted their model to the assessment estimates in Wells and Bishop (1980). It is of interest to examine the fits to the 1992 and 1993 assessment estimates. All three of the salinity terms are significantly different from zero at the 0.05 level when they are applied separately to the 1992 assessment data, explaining between 26% and 35% of the variance in estimated numbers at age 4 (Table 1). When combined in a single model 52% of the variance is explained but only salinity in year y is significant. When applied separately to the 1993 assessment estimates, s_y and s_{y+1} are significant, but s_{y+2} is not. In the combined model, only 27% of the variance is explained and none of the terms are significantly different from zero.

Myers' model

The Myers et al. (1993) model is

$$\log(\text{Recruitment}_y) = -40.4289 + 0.4281 \log(\text{SSB}_y) + 1.3741s_{y+1}$$

where SSB is spawner stock biomass (7+). The predictions from the Myers' model fitted to the 1992 assessment estimates of recruitment is compared with the 1993 assessment results in Fig. 3. The model fits the 1992 assessment estimate of 1988 recruitment poorly and the predictions diverge from the 1993 assessment estimates of recruitment after 1983. An updated fit of the Myers' model to the 1993 estimates of recruitment explains only 47% of the variance in recruitment compared to 68% with respect to the 1992 assessment and has a salinity parameter that is not significantly different from zero (Table 1). Whereas alternative models replacing s_{y+1} with s_y and s_{y+2} had salinity parameters significantly different from zero using the 1992 assessment estimates (albeit explaining less of the variance than the model with s_{y+1}), these models no longer have significant salinity terms when applied to the 1993 assessment estimates.

In Table 2 the cross validated prediction sums of squares (PSS) for regression models applied to the 1992 and 1993 assessment estimates as well as the cross validated prediction sums of squares obtained using only the arithmetic mean of the logarithm of recruitment are compared. A randomization test was carried out to determine the significance of the reduction in PSS obtained by the inclusion of salinity or spawner biomass in the model. This test comprised 200 trials in which the independent variable (annual values of salinity or spawner biomass) were randomly shuffled with respect to recruitment. For each trial the PSS was compared with that obtained with the unshuffled data. For those regression models including both s_{y+1} and SSB_y as explanatory variables, only the significance of the addition of the salinity term was tested by randomization. The proportion of cases in which the PSS value was as low or lower than that obtained from the unshuffled salinity data was interpreted as the probability that the reduction in PSS value obtained with the unshuffled data is due to chance alone. For the the 1992 assessment estimates, regression models containing only SSB_y or s_{y+1} gave PSS values substantially lower than that obtained using the mean. The PSS obtained with the model containing s_{y+1} alone was estimated by the randomization test to have a probability of 0.005 of being due to chance alone. The lowest PSS from the regression models was obtained using the Myers' model (SSB_y and s_{y+1}). The probability that the reduction in PSS obtained by including salinity is due to chance alone was estimated to be zero.

For the 1993 assessment estimates the reduction in PSS obtained by adding s_{y+1} alone or s_{y+1} in addition to SSB_y was comparatively small compared to the 1992 assessment and was not significant ($P \geq 0.05$). In contrast inclusion of SSB_y resulted in a large reduction in PSS which was found to be highly significant.

Nonparametric model

As an alternative to the regression models applied by Sutcliffe et al. (1983) and Myers et al. (1993) we followed the basic approach of Rice and Evans (1986) and applied a nonparameteric model to the recruitment data. Instead of examining the residuals from a nonparametric fit for a relationship with salinity using principal components analysis as in Rice and Evans (1986), we include salinity directly into the nonparametric model. The Cauchy distribution was used as the weighting function for both $\log(SSB_y)$ and s_{y+1} (each requiring a shape parameter to be estimated from the data). In the model including both $\log(SSB_y)$ and s_{y+1} the prediction was obtained from

$$\text{Predicted } \log(\text{Recruitment}_y) = (\text{Prediction}(\log(SSB_y)) \times \text{relwt}) + (\text{Prediction}(s_{y+1}) \times (1-\text{relwt})).$$

Parameters (the two shape parameters and relwt) that minimized the cross validated PSS were estimated by means of a grid search.

For the 1992 assessment estimates (Table 2) it is apparent that the nonparametric model including only $\log(SSB_y)$ gives a substantial and highly significant reduction in PSS compared with the mean. The addition of s_{y+1} results in only a slight further reduction in PSS which is only just significant ($P=0.045$). The nonparameteric model including both $\log(SSB_y)$ and s_{y+1} results in a PSS slightly larger than that obtained with the Myers' model.

For the 1993 assessment estimates, the nonparameteric models outperform the equivalent regression models in terms of PSS. For both regression and nonparametric models applied to the

1993 assessment estimates the reduction in PSS obtained by including s_{y+1} was found to be not significant whereas the inclusion of $\log(SSB_y)$ was highly significant (Table 2).

Discussion

There has been a substantial change in the interpretation of the role of 0-50m depth-averaged summer salinity at Station 27 as a predictor of recruitment in Div. 2J3L cod based on the 1993 assessment (Bishop et al. 1993) estimates of recruitment compared with that made by Myers et al. (1993) based on the 1992 assessment estimates (Baird et al. 1992). Sutcliffe's model (Sutcliffe et al. 1983) is shown to be a poor predictor of recruitment in recent years and to no longer fit the data when applied to either the 1992 or 1993 assessment estimates of recruitment. The salinity term in Myers' model (Myers et al. 1993) results in a significant reduction in the cross validated PSS when applied to the 1992 assessment estimates, but the reduction is not significant when applied to the 1993 assessment estimates. Likewise, the fit to the 1993 estimates gives a salinity parameter that is not significantly different from zero. For the nonparametric model including both spawner stock biomass and salinity the addition of salinity results in reduction in a PSS which is only just significant (P=0.045) when applied to the 1992 assessment estimates, but which is not significant when applied to the 1993 assessment estimates. Addition of spawner stock biomass results in a significant reduction in the PSS for both regression and nonparameteric models fitted to both the 1992 and 1993 assessment estimates.

Two obvious explanations exist for this change in the perception of the ability to predict recruitment from salinity. Either the prediction is spurious in the first place, or the 1993 assessment is considerably in error. Changes in the assessment from 1992 to 1993 are not considered remarkable. Bishop et al. (1993) state that the "...results from the current assessment, regardless of the methodology used, substantiates the previously observed declines and indicates that the stock decline has continued in 1992". Lending some credence to the suggestion that the relationship is spurious is the observation that out of the three salinity terms suggested by Sutcliffe et al. (1983), s_y, s_{y+1} and s_{y+2}, the strongest correlations tend to occur with s_{y+1} in both the Sutcliffe and Myers model. This is perplexing because it suggests that the environmental influence on recruitment is mainly operative in the juvenile stage, rather than on the egg and larval stages. Alternatively, it is possible that s_{y+1} is serving as a "surrogate" for or is "aliased with" some event that occurred in year y.

A further, more complicated explanation is that salinity was an accurate predictor of recruitment but is no longer. The departure between the Myers' model prediction and the 1993 assessment estimates commences in 1983. Although the 1993 assessment (Bishop et al. 1993) shows that spawner biomass was relatively constant at low levels between 1982 and 1988, and only declined sharply thereafter, it is possible other changes in the population influencing early stage survival commenced earlier.

A posteriori hypotheses for the observed relationships between salinity and recruitment in Div. 2J3KL cod generally invoke mechanisms which operate over several months and over large areas (e.g. Sutcliffe et al. 1983, Myers et al. 1993). Recently Helbig et al. (1992) have suggested that large scale environmental anomalies may have been overstressed and that the potential importance of smaller scale "inhomogeneities" in the oceanic environment have been ignored. As an example, numerical drift simulations that they have carried out suggest that a single storm can have a significant effect on egg and larval distribution. They conclude that subtle variations in storm

tracks could influence egg and larval survival and that large scale indices commonly used in recruitment/climate studies would be insensitive to this. Environmental inhomogeneity has interesting implications in terms of the bet-hedging traits expressed by fish populations (see Shelton 1992).

Consider survival in terms of windows in the time-space continuum (J.-L. Picard, Captain, USS Enterprise, Starfleet, United Federation of Planets, pers. comm.). The annual probability p' that any one window is open is determined by some environmental factor ω_y. If the window is open progeny located in that window all survive to become recruits; if it is closed they all die. Whether or not an individual window is open or closed is determined randomly from a binomial with $p=p'$. Let p' vary between 0 and 1 in direct response to ω_y. Assume that the time-space continuum can be discretized into a 10 window x 10 window matrix. The population has 100 progeny which it can randomly locate among windows in group sizes varying between 1 and 100 individuals. Progeny within a group all share the same fate - if the window is open they all live to become recruits; if it is closed they all die. Bet-hedging is increased by increasing the number of groups that can be allocated to windows. Simulation results for 50 years at four different levels of bet-hedging are illustrated in Fig. 4. In Fig. 4a the 100 progeny are divided into five groups of 20 individuals and each group is randomly allocated to a window. In Fig. 4b the progeny are divided into 10 groups of 10 individuals, in Fig. 4c 50 groups of 2 individuals and in Fig. 4d 100 "groups" of single individuals. Fig. 4 a to d represent increasing degrees of bet-hedging.

What is apparent from the simulation results is that the correlation between recruitment and ω_y decreases with decreasing levels of bet-hedging. Over-exploitation of a fish population may lead to reduction in mature age classes and average size of mature fish with a concomitant reduction in the number of batches of eggs spawned, the duration of the spawning season and the spatial extent of spawning. This translates into a diminished bet-hedging capability - fewer groups of progeny to be independently allocated among windows in the time-space continuum. Consequently, overexploitation could lead to a deterioration in the correlation between recruitment and an environmental index if the bet-hedging capacity of the population is affected and the environment is inhomogenous.

Although the salinity relationships of Sutcliffe et al. (1983) and Myers et al. (1993) have not held up with respect to the updated stock assessments and cannot be used as reliable predictors of future recruitment, there is strong and consistent evidence based on both the 1992 and 1993 assessments that there is a relationship between recruitment and spawner stock biomass (see also Rice and Evans, 1986; Shelton and Morgan, 1993). The cross validated PSS using spawner biomass to predict recruitment using nonparametric models is routinely found to outperform (have a lower cross validated PSS) than either the mean or geometric mean of past recruitments, and randomization tests show that the reduction in PPS as a result of including spawner stock biomass has a small probability of being due to chance alone (Shelton and Morgan 1993, Shelton and Morgan in press). For a declining spawner stock, the convention of using the geometric mean of past recruitment values in stock projections (e.g. Baird et al. 1992) is likely to be less conservative than basing the projection on the predicted recruitment from a nonparameteric model fitted to spawner stock biomass, or better still, using the probability distribution of recruitment from the nonparametric model to generate a family of projections.

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Table 1. Fit of alternative regression models to recruitment and salinity data.

Assessment	Fit years	Dependent variable	Independent variable	Prop variance explained	Probability parameter≠ 0
1992	1959-87	N age 4	s_y	0.3097	0.0017
1992	1959-87	N age 4	s_{y+1}	0.3509	0.0007
1992	1959-87	N age 4	s_{y+2}	0.2632	0.0044
1992	1959-87	N age 4	s_y	0.5195	0.0277
			s_{y+1}		0.1689
			s_{y+2}		0.0604
1992	1962-88	log(N age 3)	$\log(SSB_y)$	0.3754	0.0007
1992	1962-88	log(N age 3)	s_y	0.2492	0.0050
1992	1962-88	log(N age 3)	s_{y+1}	0.3897	0.0002
1992	1962-88	log(N age 3)	s_{y+2}	0.1540	0.0320
1992	1962-88	log(N age 3)	$\log(SSB_y)$	0.5392	0.0023
			s_y		0.0075
1992	1962-88	log(N age 3)	$\log(SSB_y)$	0.6796	0.0002
			s_{y+1}		0.0001
1992	1962-88	log(N age 3)	$\log(SSB_y)$	0.5184	0.0002
			s_{y+2}		0.0134
1993	1959-89	N age 4	s_y	0.1645	0.0262
1993	1959-89	N age 4	s_{y+1}	0.2148	0.0099
1993	1959-89	N age 4	s_{y+2}	0.1247	0.1247
1993	1959-89	N age 4	s_y	0.2730	0.2446
			s_{y+1}		0.2221
			s_{y+2}		0.4341
1993	1962-89	log(N age 3)	$\log(SSB_y)$	0.4025	0.0003
1993	1962-89	log(N age 3)	s_y	0.1032	0.0781
1993	1962-89	log(N age 3)	s_{y+1}	0.1090	0.0696
1993	1962-89	log(N age 3)	s_{y+2}	0.0583	0.1907
1993	1962-89	log(N age 3)	$\log(SSB_y)$	0.4486	0.0010
			s_y		0.1608
1993	1962-89	log(N age 3)	$\log(SSB_y)$	0.4698	0.0004
			s_{y+1}		0.0870
1993	1962-89	log(N age 3)	$\log(SSB_y)$	0.4486	0.0002
			s_{y+2}		0.1606

Table 2. Predictive ability of alternative models. The last column gives the probability of getting a prediction sums of squares (PSS) from randomly shuffled salinity or spawner stock biomass data in 200 runs that is less than or equal to that obtained from the correctly sequenced data. For models containing both spawner stock biomass and salinity, only the signficance of the additional reduction in PSS using salinity was examined by the randomization test.

Assess -ment	Model type	Dependent variable	Prediction years	Independent variables	Prediction sum of squares	Prob of getting PSS ≤ observed due to chance
1992	Mean	log(N age 3)	1962-88	-	11.5273	-
	Reg	log(N age 3)	1962-88	$\log(SSB_y)$	7.7601	0.020
	Reg	log(N age 3)	1962-88	s_{y+1}	7.1662	0.005
	Reg	log(N age 3)	1962-88	$\log(SSB_y)$, s_{y+1}	4.3290	0.000
	N-para	log(N age 3)	1962-88	$\log(SSB_y)$	4.9454	0.000
	N-para	log(N age 3)	1962-88	s_{y+1}	8.2547	0.010
	N-para	log(N age 3)	1962-88	$\log(SSB_y)$, s_{y+1}	4.4701	0.045
1993	Mean	log(N age 3)	1962-89	-	15.3629	-
	Reg	log(N age 3)	1962-89	$\log(SSB_y)$	9.9964	0.000
	Reg	log(N age 3)	1962-89	s_{y+1}	14.9132	0.395
	Reg	log(N age 3)	1962-89	$\log(SSB_y)$, s_{y+1}	9.7898	0.410
	N-para	log(N age 3)	1962-89	$\log(SSB_y)$	6.1899	0.000
	N-para	log(N age 3)	1962-89	s_{y+1}	14.6092	0.182
	N-para	log(N age 3)	1962-89	$\log(SSB_y)$, s_{y+1}	6.1638	0.130

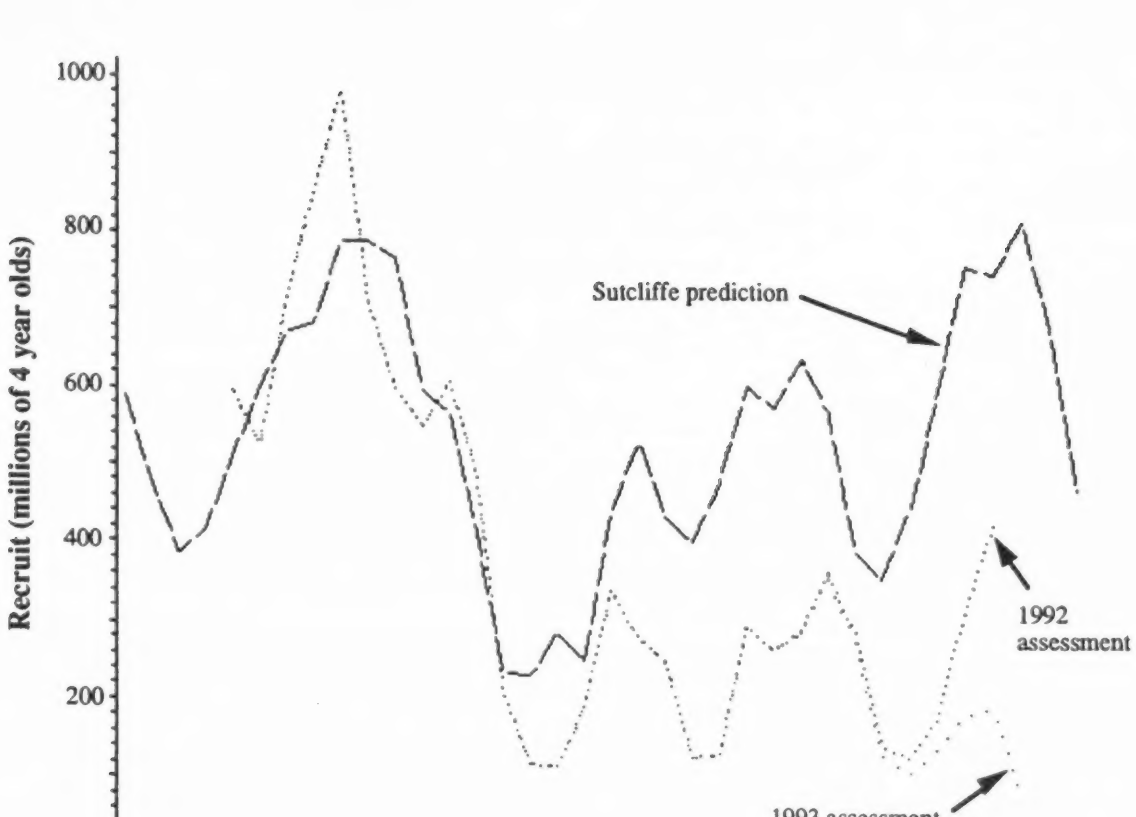

Fig. 1. Comparison of the recruitment prediction from the Sutcliffe et al. (1983) model and the 1992 and 1993 assessment estimates of number of fish at age 4 in NAFO Div. 2J3KL.

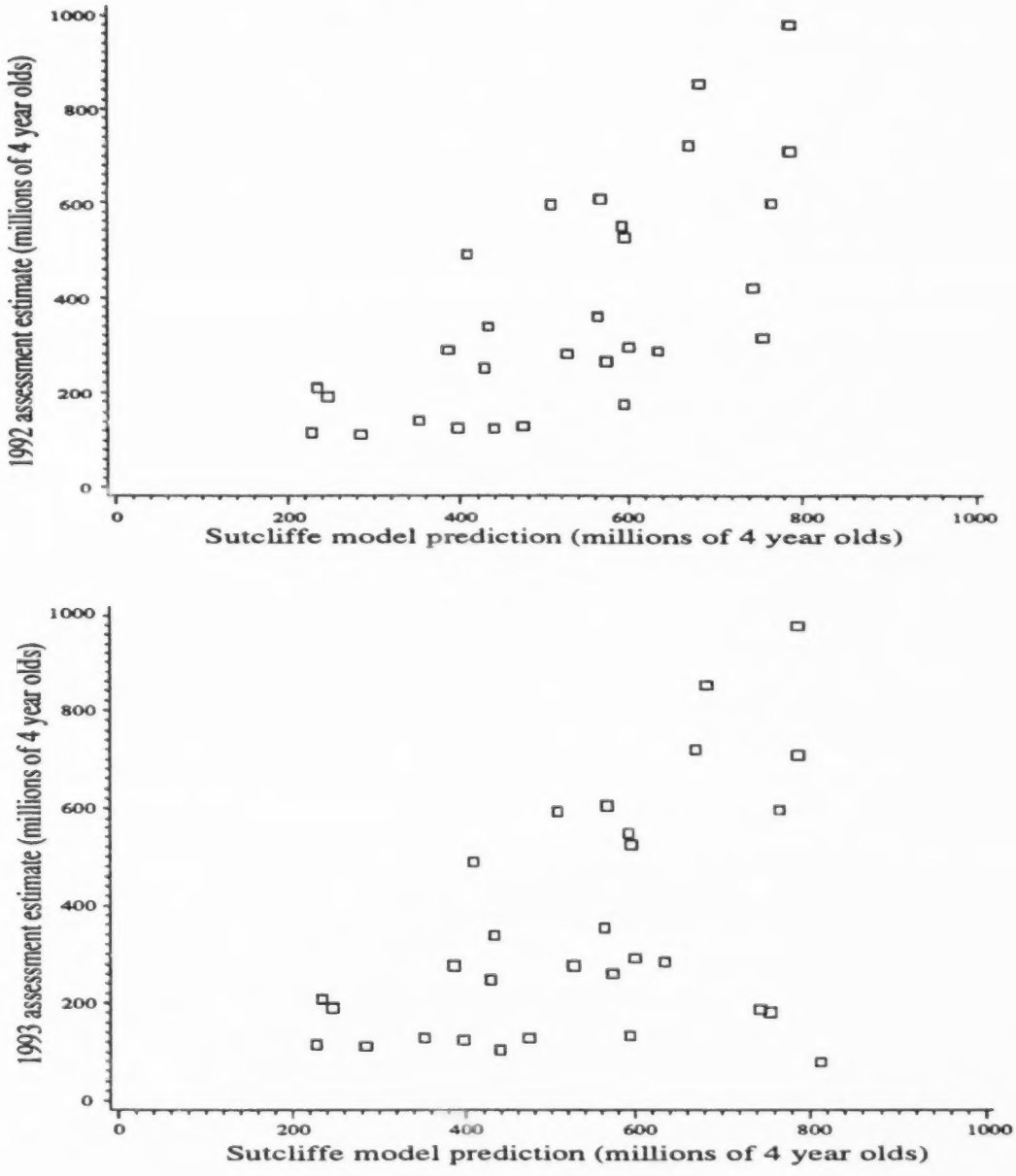

Fig. 2. Scatter plots of the 1992 and 1993 assessment estimates of recruitment and the predictions from the Sutcliffe et al. (1983) model.

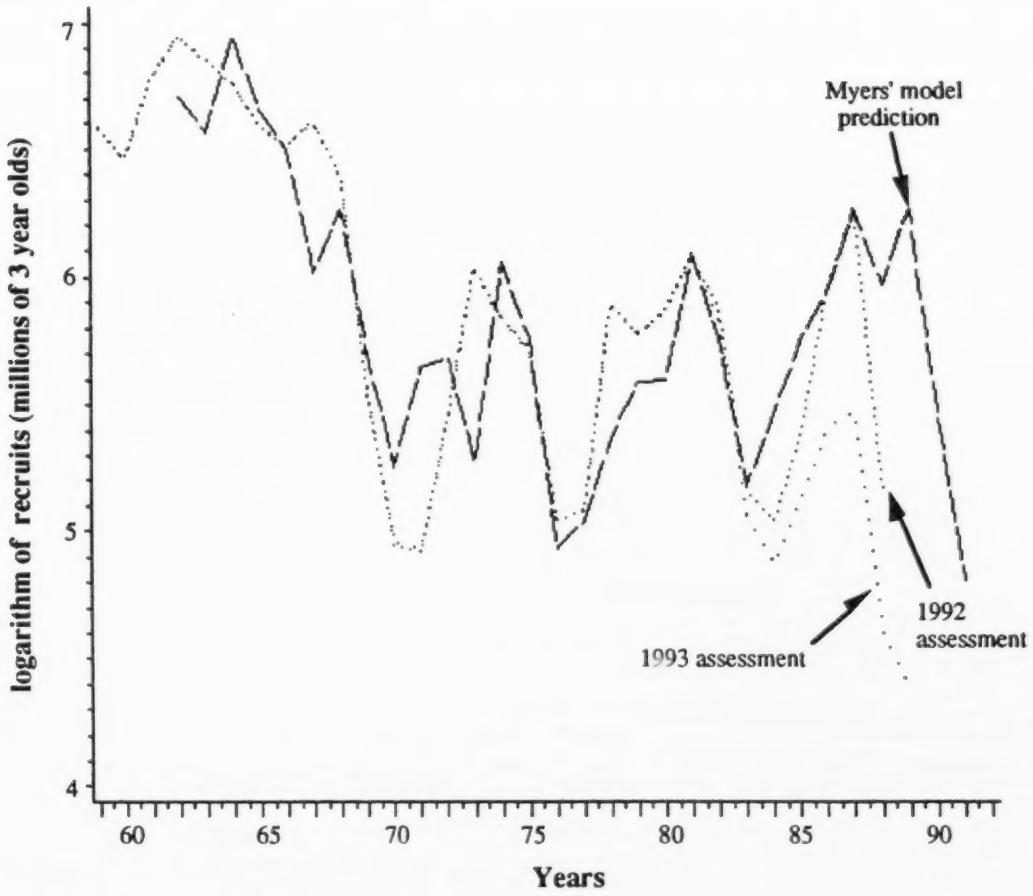

Fig. 3. Predictions from the model of Myers et al. (1993) compared with recruitment estimates from the 1992 and 1993 assessments.

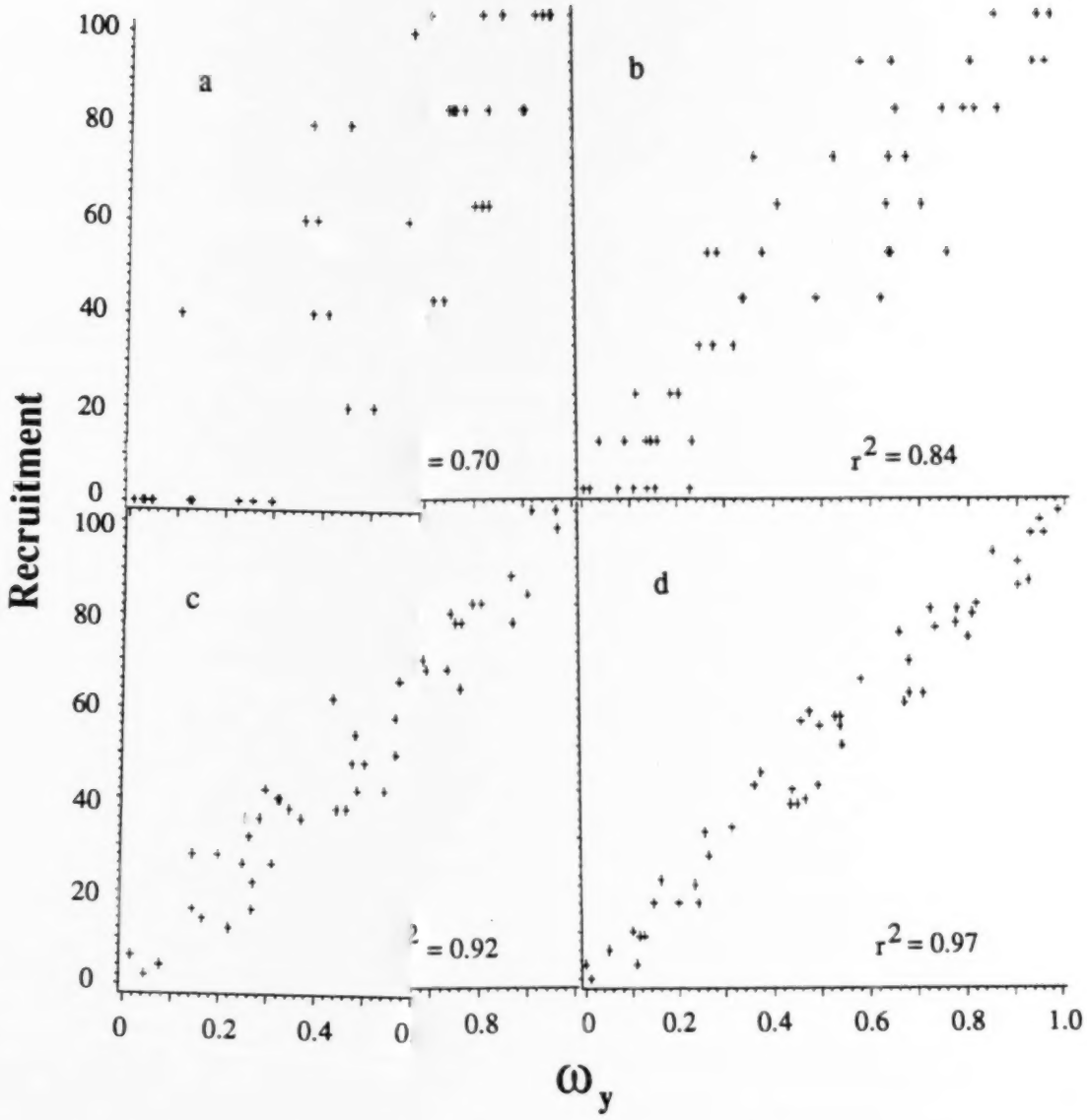

Fig. 4. Results from the simulation model to compare the correlation between recruitment and the environment (ω_y) under different levels of bet-hedging. **a** - 100 progeny are divided into five groups of 20 individuals and each group is randomly allocated to a window, **b** - 10 groups of 10 individuals, **c** - 50 groups of 2 individuals, and **d** - 100 "groups" of single individuals.